PROC. ENTOMOL. SOC. WASH.
88(4), 1986, pp. 711–719

ETHOLOGY OF *ASILUS GILVIPES* (HINE) (DIPTERA: ASILIDAE) ASSOCIATED WITH SMALL MAMMAL BURROWS IN SOUTHEASTERN WYOMING[1]

E. T. Schreiber and R. J. Lavigne

Department of Entomology, University of Wyoming, Laramie, Wyoming 86071. (ETS) Present address: Department of Entomology, Louisiana State University Center, Baton Rouge, Louisiana 70803.

Abstract.—Ethological studies reported in the literature on *Asilus gilvipes* (Hine) are fragmentary. This study gives a more complete picture of its behavior and ecology. *Asilus gilvipes* feeds, mates, and oviposits in or near the entrance to mammal burrows. The predominant prey are calliphorid flies. Males mate up to six times and females up to eight times, but the same partners were not seen to mate together more than once. Oviposition was observed, with the egg or eggs being dropped into a burrow tunnel. Larvae presumably develop in the burrows since newly emerged adults were retrieved from burrows. No burrow exposure preference to any of the eight compass orientations was noted for *A. gilvipes*. Coexistence with another burrow-inhabiting robber fly *A. formosus* is reported.

In his recent treatise on the Asilini of western United States, Martin (1975) was unable to place *Asilus gilvipes* Hine and *A. formosus* Hine in either new or existing genera. In this paper, they are retained in *Asilus* even though Martin believed that the genus does not occur in the New World. Both species are inhabitants of small mammal burrows on open rangeland (James, 1941), but behavioral and ecological information concerning the two species is fragmentary, with most observations on *A. gilvipes* (Bullington and Lavigne, 1980; Lavigne, 1968; Rogers and Lavigne, 1972). In this study we provide more complete information on *gilvipes* species and limited observations on *A. formosus.*

Methods and Study Area

Asilus gilvipes was studied 7.5 km west of the University of Wyoming campus, Laramie, in an abandoned alfalfa field close to State Highway 230 (elev. 1849 m). The study area was 9463 m^2 in size and contained a large number of Richardson ground squirrel (*Spermophilus elegans* Richardson) and badger (*Taxidea taxus* Waterhouse) burrows. The dominant plant species in the study area were: alfalfa, white top (*Cardaria draba* (L.) Desu.), and bull thistle (*Cirsium vulgare* (Savi) Tenore).

Asilus gilvipes was studied in this habitat between 25 June and 3 August during

[1] Published with the approval of the Director as paper No. JA #1316. Journal series.

the summers of 1980 and 1981. Studies were conducted from 0700 and 1800 hours daily during both summers, with specific burrow associational data and fly behavioral patterns recorded at hourly intervals. Asilids were marked individually with Testors® enamel on the prothorax for identification purposes so that each individual could be followed or subsequently located. By recapturing marked individuals, we were able to determine adult longevity, length of burrow occupancy, and whether individuals ordinarily mated more than once.

Prey records were obtained by capturing a feeding asilid in an insect net and removing the prey after the asilid dropped it. The asilid was then measured, and its sex and identification number were recorded before released. The prey was subsequently measured and identified in the laboratory.

In early June of 1981, before *gilvipes* emerged, 100 Richardson ground squirrel and 71 badger burrows were sampled for mean burrow entrance diameters and exposure of entrance slopes at eight compass orientations. These burrows were marked individually with a 5 inch nail, with identification numbers placed on the nail head. Subsequent asilid behavioral data taken from sampled burrows facilitated burrow size preference analysis.

Because the use of the burrows by the asilid may be an adaptation to a harsh environment, we were interested in determining what temperature differential existed between the soil surface and the burrow interiors. Soil temperatures were taken with a Soil Test Inc. metal thermometer (6-201), at 3 cm depth at the soil surface and at 3 cm depth in randomly selected burrows. Each day we recorded hourly the temperature of different burrows.

Results and Discussion

Seasonal distribution and abundance.—A total of 742 *gilvipes* were marked and released during the 1981 season. Of these, 451 (61%) were recaptured or observed on one or more days within the study area. Marked flies showed a strong affinity for the study area throughout the season. Sampling outside the immediate study area revealed the presence of only two marked specimens.

Following marking, individuals survived an average of 17 days; the longest lived individual was recaptured after 23 days (Fig. 1). This suggests that adult flies normally survive for approximately three weeks. Similar findings for this species were found by Rogers and Lavigne (1972) in northeastern Colorado.

Asilus gilvipes is a short lived early/midsummer species in southeastern Wyoming (Fig. 2). In 1981 the first adults appeared on 25 June (4 ♀, 1 ♂ Emergence continued over a short span of time with the population peaking on 10 July (25 ♀, 33 ♂). The population remained at high density through mid-July and then decreased; a secondary peak in abundance was noted on 25 July (20 ♀, 16 ♂), followed by a steady decline with no individuals recovered after 2 August. Censuses conducted the previous year provided similar results for population abundance and time of last adult sighting.

Recaptures of *gilvipes* were most numerous around mid-July when individuals were most abundant. Daily sampling showed that as the population rose and fell, sexual density followed the population curve; the ratio of one sex to the other remained the same (49:51%, N= 742) throughout the season (χ^2= 3.1 N.S.). For *Edioctria tibialis* Banks, however, Scarbrough (1981) found that males were more abundant than females during the early half of the season, whereas the reverse was true in the latter half.

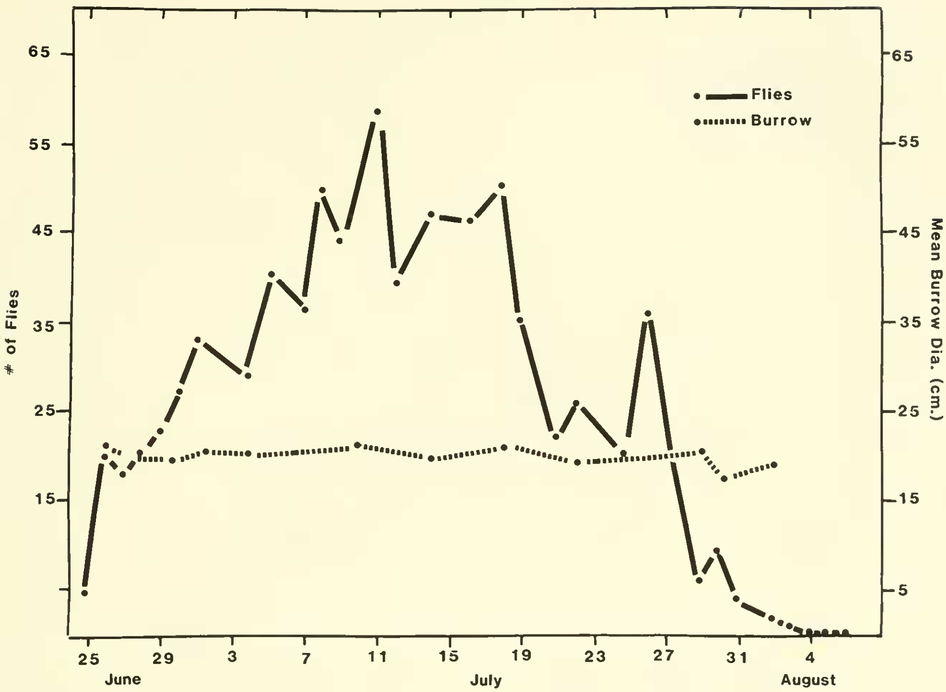

Fig. 1. Relative abundance of *Asilus gilvipes* and mean burrow diameter.

Diurnal behavior.—On most days, *gilvipes* was found resting either within burrows or on the outer rim. Individuals would remain associated with a specific burrow for varying numbers of days. The longest association was 3 days.

Predation was the most common activity observed during most daylight hours with the exception of 1300–1400 h when mating behavior was dominant (Fig. 3). Predation took place within the confines of the burrow when burrow temperatures ranged from 16.5–27.0°C. The peaks of predatory activity occurred at 1100–1200 h and again at 1400 to 1500 h MDT. These peaks, which correspond to soil surface temperatures of 21–33° and 23–36°C, may be associated with increased density of potential prey within the burrows. We postulated that these insects were escaping from high outside temperatures by entering the burrows (Lavigne, 1968). The majority of prey were taken while they were in flight within the burrow, but insects were also captured as they entered and left the burrow.

Grasshopper nymphs were also taken as prey. Apparently these wingless insects were captured while resting on the burrow walls. To test this assumption, a tabanid fly, *Tabanus* sp., was captured and one of its wings removed. The tabanid was then placed on the inside rim of a *gilvipes*-occupied burrow. Twenty-two minutes later a specimen of *gilvipes* was found feeding on the tabanid.

Following is a description of a typical predatory act recorded on 12 July 1980.

3:22 pm A *gilvipes* female observed in a badger burrow with a western exposure (entrance diameter of approx. 15 cm); hovers within burrow and captures a flying calliphorid; flies to northern rim. The prey is impaled on the hypopharynx and held by the midlegs.

Fig. 2. Numbers of *A. gilvipes* recaptured one or more day(s) following mark and release.

3:22:30	Hovers; moves hypopharynx to dorsum of prey's thorax and returns to burrow wall.
3:27	Hovers; places hypopharynx in the ventral portion of calliphorid's abdomen, returns to burrow wall.
3:31	Hovers; places hypopharynx in the pleurnal section of the thorax; returns to burrow wall surface.
3:46:30	Hovers; shifts hypopharnyx to venter of abdomen; returns to burrow wall; ballooning of prey evident.
3:57	Hovers; moves hypopharynx to venter of thorax; returns to burrow wall.
4:09:15	Hovers; shifts hypopharnyx to dorsal tip of abdomen.
4:19	Prey falls off hypopharnyx; no tarsal assistance.

Complete feedings from capture to release were observed for 15 prey. The mean feeding time was 43 minutes, ranging from 5–72 minutes in duration. The majority of prey taken were Diptera (Tables 1–2); these were primarily *Phormia regina* Meigen. Diptera were 33% of the prey of *Asilus mesae* (Tucker) (Rogers and Lavigne, 1972). Dennis and Lavigne (1975) found that Diptera made up 18.6% of the prey of *A. mesae.*

Because there was an apparent specificity for one group of flies, the authors proposed the following hypothesis. Calliphorids deposit eggs on dead carcasses

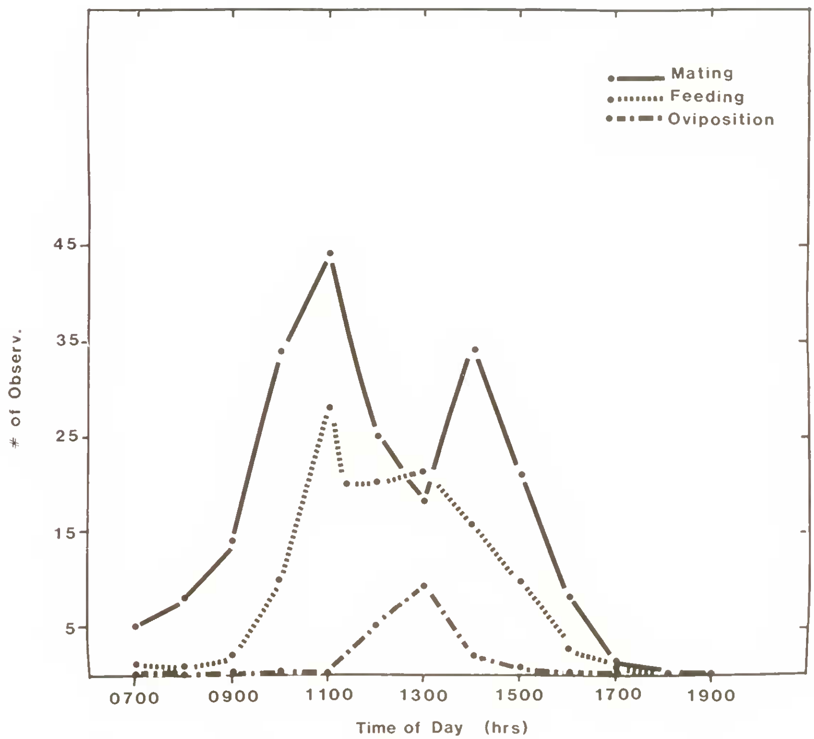

Fig. 3. Diurnal rhythm of mating, feeding, and ovipositional activity of *Asilus gilvipes* (mating N = 111, feeding N = 212, oviposition N = 171).

and other decaying organic materials, such as feces (Hall, 1948). Badgers and ground squirrels are known to defecate in and near their burrows (F. Lindzey, Utah State University, pers. comm.; Sargent and Warner, 1972; Messick and Hornocker, 1981). It follows that calliphorids have a high selection value because they are attracted to dung and/or to odors emanating from it, thus increasing the density of flies in the burrow microhabitat.

As a preliminary test we attempted to associate mammal burrow occupancy with burrow visitation by calliphorids. To detect burrow occupation by mammals, an experiment was conducted in which grass stalks were placed upright about 6 cm deep in burrow tunnels occupied by *A. gilvipes* during that day. This method has been used by some badger ethologists to check for burrow occupancy (Lindzey, 1978). The following morning the grass stalks were checked to see if they had remained upright. A total of 25 badger burrows were "grass stalked" on 8 July 1981. The following morning, 9 July, stalks in 18 burrows were knocked down. This preliminary test indicated that the burrows were occupied, but did not definitely identify the species of mammal inhabiting them, since ground squirrels have been known to inhabit badger burrows (H. Harlow, Univ. of Wyoming, pers. comm.). On 10 July two artificial burrows were dug measuring 8–10 cm in depth with burrow diameters of 11 cm and 13 cm, respectively. Fresh dung pellets were collected from ground squirrel-occupied burrows and placed in one of the burrows. Dung from ground squirrels was utilized because of its abundance, freshness and

Table 1. Number and percent composition of prey by insect order taken by *Asilus gilvipes.*

Order	Male		Female		Total	
	Number	Percent	Number	Percent	Number	Percent
Coleoptera	5	6.0	6	5.0	11	5.4
Diptera	72	86.7	106	88.3	178	87.7
Hymenoptera	5	6.0	2	0.6	7	3.4
Orthoptera	1	1.4	6	5.0	7	3.4
Total	83	99.7	120	99.9	203	99.9

availability (badger dung is placed in special pockets in the burrow itself by the badger (Messick and Hornocker, 1981) whereas ground squirrel dung is available at the burrow entrance). Calliphorids on the rim and within each burrow, one containing feces and the other not, were counted hourly throughout the day. On the following day, fresh dung was placed in the burrow lacking it and the previous day's dung was removed from the burrow which had contained it. Calliphorid and muscoid flies were observed only in the artificial burrow containing the dung. This simple experiment, although not replicated, suggests that the high number of calliphorid flies in the diet of this species of asilid is due to the propensity of these flies to congregate in the vicinity of dung, a behavior to which the asilids appear to have adapted successfully.

The mean predator to prey size ratio for this species is 2.03:1 (Table 3), based on length. Females, though not significantly larger than males took similar sized prey which resulted in a significantly greater prey ratio for them. While *Efferia frewingi* females have been shown to be more discriminate than males in prey choice based on models presented to both sexes (Dennis et al., 1975), the data in Table 4 suggest that this is not the case for *A. gilvipes.* Females in fact appear to be less discriminatory, especially for the larger size class. However, the 15.1+ mm size class are two reports of cannibalism by females on males.

Reports of cannibalism are not unusual among the Asilidae (Lavigne and Dennis, 1975; Rogers and Lavigne, 1972; Lavigne and Holland, 1969) but its cause is obscure. Fox (1975), in discussing cannibalism in general, states that it is not an "aberrant behavior" limited to stressed populations, but a normal response to many environmental factors. Intense crowding is one factor suggested by Fox but such was not the case in this study. The availability of potential prey may be the

Table 2. Number and percentage of Diptera prey taken by *Asilus gilvipes.*

Family	Male		Female		Total	
	Number	Percent	Number	Percent	Number	Percent
Anthomyiidae	2	1.1	1	0.5	3	1.6
Asilidae	2	1.1	3	1.6	5	2.8
Calliphoridae	61	34.3	90	50.5	151	84.8
Muscidae	—	0.0	5	2.8	5	2.8
Therevidae	1	0.5	1	0.5	2	1.1
Sarcophagidae	2	1.1	3	1.6	5	2.8
Undet. Diptera	4	2.2	3	1.6	7	3.9

Table 3. Relation between length of *Asilus gilvipes* and that of its prey.

Sex	Predator Length (mm)[1]			Prey Length (mm)			No. of Prey Measured	Mean Ratio of Predator to Prey
	Min.	Max.	Mean	Min.	Max.	Mean		
Male	14.0	21.0	17.00	3.50	13.50	8.54	61	1.99[b]
Female	17.0	23.0	18.20[a]	3.00	17.20	8.65	96	2.10[c]
Total	14.0	23.0	17.60	3.0	17.20	8.60	157	2.03

[1] 45 measured of each sex.
[a] Not significant difference; $P = .05$ df 44.
[b] Significant difference; $P \leqq .05$ utilizing *t*-test approx. variance formula for a ratio.
[c] Significant difference; $P \leqq .05$ utilizing *t*-test approx. variance formula for a ratio.

more valid reason. *Asilus gilvipes* females were observed to feed on the males when population density was low (24 July). Many of the burrows at this time were poorly maintained, indicating less burrowing rodent activity in the area. This could have resulted in fewer visits by coprophagous flies. Additionally, calliphorid prey records were fewer late in the asilid season.

Mating behavior.—Mating behavior of *A. gilvipes*, tail to tail in this species, has been described in detail previously by Bullington and Lavigne (1980). Twelve complete matings of *A. gilvipes* were observed during the present study. They ranged from 18 to 42 min. in duration with the mean being 26.5 min.

Multiple mating as observed by Bullington and Lavigne (1980) appears to be a common behavioral attribute of this species. Sixty marked males were observed to mate from 1 to 6 times, a mean of 1.33 mating/male. Additionally, 53 marked mated females were recorded mating 1 to 8 times for a mean of 1.47 matings/female, but no instances are recorded of the same male and female remating.

Oviposition behavior.—Following 48 observed matings, females oviposited immediately in only 20 instances. Those that did may have mated previously.

While resting on the rim of the burrow, the female drops eggs either singly or in small packets of three into the burrow tunnel. The time spent ovipositing by females ranged from 2–12 min. (mean 3.5 min.). The eggs presumably hatch within the burrow and the larvae feed within the burrow until pupation. Two newly emerged *A. gilvipes* adults were seen to emerge from badger burrows (4 July, 8 July 1981); pupal cases were recovered from the burrow.

Burrow preference.—Since *Asilus gilvipes* is intimately associated with mammal burrows, it was of interest to determine if the flies exhibited preference for certain types of burrows. Marked individuals were associated for varying time periods with 133 burrows. Of these, 15 asilids were found in ground squirrel burrows and 116 in badger burrows. The average diameter of the entrance of ground squirrel

Table 4. Size class percentage of prey of *Asilus gilvipes* by sex.

Sex	Prey Size				Total Prey
	3.1–7.0 (mm)	7.1–11.0 (mm)	11.1–15.0 (mm)	15.1+ mm	
Male	17.0%	79.0%	3.0	0.0%	61
Female	21.0%	74.0%	3.0	2.0%	96
Avg. total %	19.0%	76.5%	3.0%	1.0%	157

Table 5. Chi-square 8 × 2 contingency table test results comparing expected frequencies with observed frequencies for burrow occupation of *Asilus gilvipes* at eight compass orientations.

	N	NW	NE	S	SW	SE	E	W
Observ. bur.	42.00	16.00	18.00	27.00	19.00	12.00	48.00	53.00
Expected bur.	49.58	14.16	15.45	28.97	14.81	12.23	44.42	55.37
Ob. *A. gilvipes*	35.00	6.00	6.00	18.00	4.00	7.00	21.00	33.00
Ex. *A. gilvipes*	27.42	7.84	8.55	16.03	8.19	6.77	24.58	30.63

$\chi^2 = 9.9113$, df = 7, $P = .05$.

burrows was 12.80 cm and that of badger burrows was 20.54 cm, for an overall average of 18.69 cm. No correlation was found between the expansion of the size of the population and the choice of burrow (Fig. 1). We assume this to mean that there were always more burrows available than flies present, so no inter- or intraspecific competition for burrows occurred.

Additionally we were interested in knowing whether there was any correlation between compass direction of the burrow entrance and the choice of burrow made by *A. gilvipes.* In Table 5, an 8 by 2 contingency table of burrow occupancy by *A. gilvipes* at eight compass orientations shows that no preference for any burrow exposure existed ($P > 0.05$). Lavigne (1968) and Rogers and Lavigne (1972) stated that asilids use burrows to escape the heat. We find that burrows are used in times of high winds and storms as shelters, as well as during periods of high air temperatures.

Species coexistence.—Only one other species of robber fly, *A. formosus* Hine, utilized burrows on the same study site. This species was previously described as a burrow resident by Rogers and Lavigne (1972) in northeastern Colorado. They speculated that coexistence of the two species of asilids might occur under the right circumstances. While the two species occupy the same burrows in the same habitat, they differ in their seasonal occurrence. *Asilus gilvipes* is present from 25 June to 3 August, whereas *A. formosus* is present from 12 July to late August. They also differ in size, with *A. gilvipes* at 17.60 mm in length, being significantly larger than *A. formosus* (14.50 mm) ($P < 0.05$ *t*-test). This size difference allows the two species to share the available prey, with *A. gilvipes* taking the larger prey items. There also exists a significant difference in the mean diameter of the burrow opening chosen by each species: those of *A. gilvipes* measure 18.69 cm, whereas *A. formosus* inhabits burrows measuring 10.32 cm in diameter. Consequently, it appears that these two species can be present in the same habitat because they differ in seasonal occurrence, size, and burrow preference. Similar coexistence strategies with respect to robber flies have been noted by other authors (Dennis and Lavigne, 1975; Lavigne and Holland, 1969; Rogers and Lavigne, 1972; Scarbrough, 1981).

Literature Cited

Bullington, S. W. and R. J. Lavigne. 1980. An instance of multiple mating in *Asilus gilvipes* (Diptera: Asilidae). Pan-Pac. Entomol. 56: 79–80.

Dennis, D. S. and R. J. Lavigne. 1975. Comparative behavior of Wyoming robber flies II. (Diptera: Asilidae). Univ. Wyoming Agric. Exp. Stn. Monogr. 30. 68 pp.

Dennis, D. S., G. P. Rochrkasse, and R. J. Lavigne. 1975. Prey recognition by *Efferia frewingi* (Diptera: Asilidae). Ann. Entomol. Soc. Am. 68: 404–408.

Fox, L. R. 1975. Cannibalism in natural populations. Ann. Rev. Ecol. Syst. 6: 87–106.

Hall, D. G. 1948. The blow flies of North America. Thomas Say Foundation Publ. 4 V + 477 pp., 5 col. pl. 46 pl., 9f.

James, M. T. 1941. The robber flies of Colorado (Diptera: Asilidae). J. Kans. Entomol. Soc. 14: 27–53.

Lavigne, R. J. 1968. Notes on two species of *Asilus* (Diptera: Asilidae) associated with animal burrows with a redescription of *Asilus gilvipes* Hine. J. Kans. Entomol. Soc. 41: 334–339.

Lavigne, R. J. and D. S. Dennis. 1975. Ethology of *Efferia frewingi* (Diptera: Asilidae). Ann. Entomol. Soc. Am. 68: 992–996.

Lavigne, R. J. and F. R. Holland. 1969. Comparative behavior of eleven species of Wyoming robber flies (Diptera: Asilidae). Univ. Wyoming Agric. Exp. Stn. Sci. Monogr. No. 18. 61 pp.

Lindzey, F. G. 1978. Movement patterns of badgers in northwestern Utah. J. Wildl. Manage. 42: 418–422.

Martin, C. H. 1975. The generic and specific characters of four old and six new Asilini genera in the western United States, Mexico, and Central America (Diptera: Asilidae). Occ. Pap. Calif. Acad. Sci., No. 119. 107 pp.

Messick, J. P. and M. G. Hornocker. 1981. Ecology of the badger in southwestern Idaho. Wildl. Monogr. No. 76. 53 pp.

Rogers, L. E. and R. J. Lavigne. 1972. Asilidae of the Pawnee National Grasslands in northeastern Colorado. Univ. Wyoming Agric. Exp. Stn. Sci. Monogr. No. 25. 35 pp.

Sargent, A. B. and D. W. Warner. 1972. Movements and denning habits of a badger. J. Mammal. 53: 207–210.

Scarbrough, A. G. 1981. Ethology of *Eudioctria tibalis* Banks (Diptera: Asilidae) in Maryland: Seasonal distribution, abundance, diurnal movements, and behaviors. Proc. Entomol. Soc. Wash. 83: 245–257.